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Contribution to the Bionomics of *Ceramius tuberculifer* Saussure (Hymenoptera, Vespidae, Masarinae)

VOLKER MAUSS

2. Zoologisches Institut und Museum der Georg-August-Universität, Berliner Straße 28, D-37073 Göttingen, Germany

Abstract.—Three nesting aggregations of *Ceramius tuberculifer* Saussure were investigated in the French Alps. *C. tuberculifer* inhabits submediterranean calcareous grassland. The nest consists of a one- to multi-cellular burrow surmounted by a mud turret. The main shaft descends obliquely into the ground and terminates in a cell. Secondary shafts are short. Brood-cells are built of mud within an excavated cell. Nests are probably perennial. Imagines are polylectic, collecting primarily pollen from *Teucrium montanum* L. (Lamiaceae), *Helianthemum* (Cistaceae) and an unidentified Fabaceae. There are additional flower visiting records from *Lavandula* (Lamiaceae) and *Ononis*. (Fabaceae). The imagines employ a specialized method to gather pollen from *Teucrium*-flowers, which can be interpreted as a behavioural adaptation to a nototribic pollen presentation. Males patrol along flight paths in the foraging area of the females. They interrupt their flight regularly in order to perch for short periods. *Chrysis emarginatula* Spinola (Chrysididae) is a common parasitoid. Larvae of *Zodion* (Conopidae) and Mermithidae (Nematoda) were identified as endoparasites of the imagines.

INTRODUCTION

The genus *Ceramius* Latreille is a monophyletic subgroup of the honeywasps (Masarinae) (Carpenter 1993). All species studied so far are solitary (Gess & Gess 1989, 1990). They nest in the ground in excavated burrows, which are surmounted by a mud entrance turret. The brood-cells are provisioned with a mixture of pollen and nectar (Gess & Gess 1989, 1990). Based on morphological characters and biogeographical evidence *Ceramius* has been divided into eight species groups (Richards 1962) one of which has recently been subdivided (Gess & Gess 1988). Moreover, Gess & Gess (1986, 1988, 1990) have shown for the Afrotropical taxa (the species groups 2, 3, 4, 5, 6, 8 of Richards 1962) that there are specific differences between the species groups in regard to nest-construction and flower visiting. Hitherto, comparable information on the bionomy of the palaearctic *Ceramius*-species (groups 1 and 7) has not been recorded (cf. Gess & Gess 1988). *Ceramius tuberculifer* is a member of species group 7 (Richards 1962). The species has been found in southern France and in the northeastern parts of the Iberian Peninsula (Richards 1963). It is closely related to *C. lusitanicus* Klug, *C. vechti* Richards and *C. bischoffi* Richards, with which it had been united under the name *C. lusitanicus* until the revision by Richards (1962, 1963). Giraud (1871) and Ferton (1901) described habitat and nest-construction of *Ceramius tuberculifer* in the French Alps and the Pyrenees, respectively. Whether Ferton's account really refers to *C. tuberculifer*, as supposed by Richards (1962), is uncertain. The observations of Giraud (1871) and Ferton (1901) are to some extent at variance with each other.

In the following data about habitat, nest construction, flower visiting, pollen collecting, mating and parasites of *C. tuberculifer* are presented which were obtained at nesting aggregations in South France.

The results are compared with descriptions of other *Ceramius*-species.

MATERIAL AND METHODS

Investigations were carried out from 19 to 29 July 1994. Weather conditions were almost uniform throughout the whole period. Until about midday it was sunny and temperatures rose to 25°–30°C. Later in the day it clouded over, and more than once there were fairly heavy thunderstorms. In the upper valley of the Verdon river (Département Alpes Haute Provence), open habitats in the vicinity of la Foux d'Allos, Allos, Colmars, Beauvezer, Peyresq, Thorame-Haute, Thorame-Basse and la Valette were sampled for imagines and nests. The nesting area at Peyresq was visited on July 19, 21, 25 and 28, July, that on the Montagne de Boules on 26 and 29 July. Observations were noted in the field and documented using a 35 mm camera with 100 mm lens (scale up to 1:1) and flash. Time is Central European Time. Positions of the nests in the nesting aggregations were recorded as sketches, which were retouched later by comparing them with photos taken at the time. Five nests were excavated. Their construction was outlined as accurately as possible, although exact measurements could not be taken due to the nature of the soil. Entire brood-cells were collected and later studied under a dissecting microscope. Plants which had been visited by adults were preserved both dried and in 70% ethanol. Samples of *C. tuberculifer* were collected, 10 males and 29 females at Peyresq and one male and one female on the Montagne de Boules. The metasomata of all specimens were dissected under a dissecting microscope and examined for endoparasites. The alimentary tracts of six females from Peyresq were fixed according to the formula of Pabst & Crailsheim (1990). Then pollen samples from the ventriculus and the rectum were prepared using the method of Westrich & Schmidt (1986). The pollen was determined under a light microscope and compared with pollen from the anthers of the ethanol-fixed plants prepared in the same way. Only pollen-types that existed in large quantities were considered for the evaluation. Quantitative indications were estimated. In each case, five of the ethanol preserved males and females were selected at random to investigate the pollen-distribution on the exoskeleton. The number of grains on the clypeus, the vertex + frons, the rest of the head, the dorsal, left, right and ventral part of the mesosoma, the fore-, middle- and hind-legs and the metasomal-tergites and -sternites were counted separately under a dissecting microscope. From these data, the total number of pollen grains was summed up for each specimen and the proportional number of grains on vertex + frons, the dorsal part of the mesosoma and the rest of the body was calculated. Finally, the arithmetic means and their standard errors of the proportional numbers for males and females were calculated.

BIONOMIC ACCOUNT

Description of the Habitats.—*Ceramius tuberculifer* was found at two localities in the vicinity of Thorame-Haute, which are characterized in more detail in Table 1. Both were in submediterranean calcareous grassland (Brometalia Br.-Bl.). The ground cover was about 60–70%. In both localities *Teucrium montanum* (Lamiaceae) was strikingly more abundant than in the surrounding areas. The soil, in which the burrows were excavated, contained some clay and was somewhat friable.

At Peyresq the ground was partially covered with clusters of approximately 0.3 m high *Sarothamnus*-(Fabaceae) and *Lavandula angustifolia* Miller (Lamiaceae) shrubs and a few pines of 1–(3)m in height (Fig. 1). Among the dwarf shrubs, the soil was sparsely covered with low vegetation dominated by *T. montanum* and grasses. One nesting aggregation (= aggregation P) with 77 nests was located on an area of

Table 1. Characters of two localities with nesting aggregations of *Ceramius tuberculifer* in the vicinity of Thorame-Haute (France: Département Alpes Haute Provence)

Parameter	Peyresq	Montagne de Boules
location	a little up-hill from the D.32 about 400 m before Peyresq	about 2 km NNW from la Valette
co-ordinates (Gauß-Krüger)	44°4′22″N 6°36′46″E	44°9′29″N 6°30′31″E
altitude above sea-level	1520 m	1560 m
exposition of the slope	250°	150°
approx. steepness of the slope	10°	45°
outset from sun-irradiation	9h00	6h00
minimal distance towards the next water-site	300 m (stream in the valley)	200 m (stream in the valley)

about 10 m^2, where the soil contained slightly more clay than in the surroundings. Most of the nests were in sparsely covered soil, only five were under a little *Sarothamnus* bush (Fig. 3). In the centre of the aggregation, the nest-entrances were close to one another, with minimum distances of approximately 50 mm. Towards the edges the space between nests increased (Fig. 3). About 15 m northeast of the aggregation an isolated nest was found. The adults visited flowers mainly in an area that extended 30–100m in a northeasterly direction from the aggregation (Fig. 1), where *T. montanum* occurred abundantly and *Helianthemum oelandicum* L. (Cistaceae) less so.

On the Montagne de Boules two nesting aggregations (= aggregations B1 and B2) were found on a steep slope, which was cut by numerous bare, dry erosion-rills, many of which were filled with gravel (Fig. 2, Table 1). Vegetation was more diverse than at Peyresq. Predominantly 0.3–0.5 m high grasses, *Sarothamnus, Lavandula* and a yellow flowered species of Asteraceae were growing among scattered pines of 0.5–3 m in height. Furthermore, *T. montanum* and on a smaller scale *H. oelandicum, Ononis fructicosa* L. (Fabaceae) and *Campanula* spec. (Campanulaceae) occurred. The calcareous grassland was bordered by pine-forest at three sides. Obliquely up hill it continued into a steep open area of larger dimensions. The aggregations were located in the middle of the slope (Fig. 2). The distance between them was about 10 m. The more westerly aggregation B1 consisted of 25 nests, B2 of 13. Most of the nests were established at restricted spots directly below plants, which were protected against erosion (Fig. 4). At these places, the root-system detained weakly clayey soil, in which the burrows were excavated. At suitable sites the shortest distances between the nests were approximately 50 mm. Foraging adults were observed about 25 m northeast of aggregation B2, where *Teucrium montanum* was flowering in abundance.

Nest Construction.—Some of the nest-entrances were surmounted by a more or less damaged cylindrical turret which was constructed from mud pellets cemented together. The best preserved turret was approximately 15 mm long (Fig. 5). Initially it was subvertical, but after half of its length it curved over becoming horizontal. The walls had no interstices. Often only remnants of a turret were present. Frequently, there was no indication of a turret at all (e.g. in 34 nests of B1 and B2). During the observation period neither construction nor repair of a turret was seen.

Vertical plans of the burrows are presented in Fig. 6 and the contents of each nest are listed in Table 2. In all nests the

Figs. 1–2. Fig. 1. Nesting area of *Ceramius tuberculifer* at Peyresq, 28.7.1994; view from the southwest. The nesting aggregation P was situated in front of the two little pines a bit to the right from the centre (arrow). The foraging area of the imagines extended in front of the pine forest fringe on the left. Fig. 2. Habitat of *Ceramius tuberculifer* on the Montagne de Boules, 26.7.1995; view from southeast. The nesting aggregations B1 and B2 were in the centre of the steep slope. Flower visiting females were commonly observed in an adjacent open area obliquely uphill to the right.

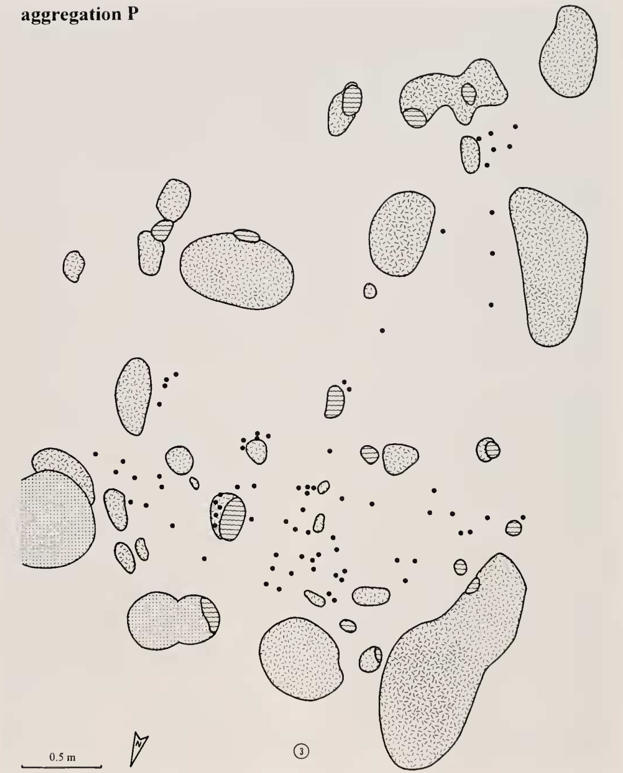

Fig. 3. Positions of the nests in the nesting aggregation P of *Ceramius tuberculifer* at Peyresq, 21.7.1994. For key see Fig. 4.

entrance was followed by a shaft of constant diameter descending 50–70 mm obliquely into the ground. Whenever brood-cells were present, the shaft terminated in a cell (Fig. 6). When there was more than one cell, they were closely grouped. Most of the cells lay sub-horizontally, one cell was orientated downwards. All cell-openings were directed towards the end of the shaft.

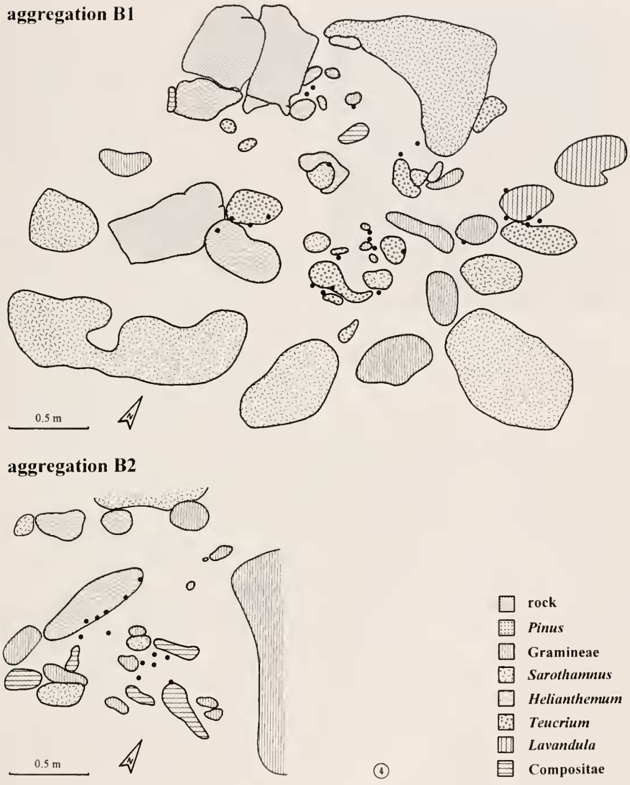

Fig. 4. Positions of the nests in the nesting aggregations B1 and B2 of *Ceramius tuberculifer* on the Montagne de Boules, 26.7.1994.

The constructed mud brood-cells were easily separated from the adherent soil. They varied from nearly cylindrical to bean-shaped (Fig. 9). They had a rough, irregular outer surface on which separate applications of mud were discernible. The inner surface was regular and smooth but dull. Fragments of fibrous tissue and

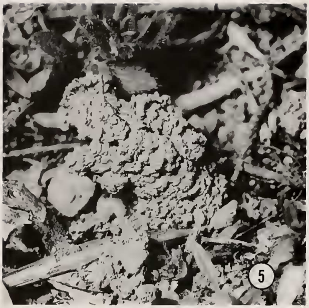

Fig. 5. Mud turret surmounting the entrance of a *Ceramius tuberculifer* nest; Peyresq 21.7.1994 (length of the turret approximately 15 mm, its distal parts are slightly damaged).

threads corresponding in structure and colour to cocoon-material (see below) were embedded in the walls and mud-plugs of two cells of nest 5. Similar fragments and fibres mixed with crumbly soil were found within the cocoon of nest 4.

Three cells of nest 5 were studied in detail (Fig. 7). They measured 18–23 mm in length and had a maximum outer diameter of approximately 11 mm. Their walls were 1.1–1.9 mm thick. The cells were sealed with a 3.0–3.5 mm long mud plug at the proximal end. The cocoon-cap was located close behind the plug, but separated from it by a very short empty space. The cap was a circular weakly biconcave plate, from 4.3 to 4.7 mm in diameter. The cocoon consisted of reddish to brownish, slightly shining fibrous tissue. It was 14–17 mm long and 5.8–6.6 mm wide at its greatest, and the distal end was rounded. The cocoon was in intimate contact with the inner walls of the mud cell from which it could be parted only with difficulty. There were small black brownish shining pellets on the inner surface of the cocoon in an annular zone of 1 mm in length, 2–4 mm distal from the cocoon-cap. The hollow hemispherical pellets had thin brittle walls which consisted of a substance that was homogeneously brownish and translucent under the light microscope. In their outer appearance the pellets resembled the "fecal pellets" from *Pseudomasaris edwardsii* (Cresson) (Masarinae) (cf. Torchio 1970). In one case these pellets were in addition present at the distal end on the inner surface of the cocoon. Starting at 6.0–7.5 mm distal from the cap and extending from there over the whole distal portion of the cocoon a thin, yellowish, slightly granular and brittle layer covered the inner wall of the cocoon. The light microscope revealed that it consisted of pollen-exines, which were tightly compressed and united with a secretion.

Behaviour of the Females.—Females were regularly observed excavating their nests. They backed up the shaft with a soil-pellet held by their mandibles. The pellets were nearly half as large as their heads (Fig. 8). As soon as they had left the nest entrance, the females turned 90°–180° on their vertical axis and discarded the pellet (cf. Fig. 8). Then they turned back and re-entered the nest head first. The earth was always dropped at the same spot a few centimetres from the entrance, where a small heap was formed. Judging from its appearance, the soil on the heap was moist. I did not discover if or to what extent liquid was used in order to soften the ground in the course of nest excavation. Transport of water in the crop was not observed but the crops of two females collected at aggregation P were tensely filled with a clear liquid of high viscosity, probably nectar.

Before activity started in the morning and during times of unfavourable weather the females rested in the upper part of the shaft, each with its head directed to the entrance and completely plugging the shaft. As an exception one female was observed crawling under the twigs of a *Teucrium* plant as the sky became overcast. It remained there, lying more or less on its

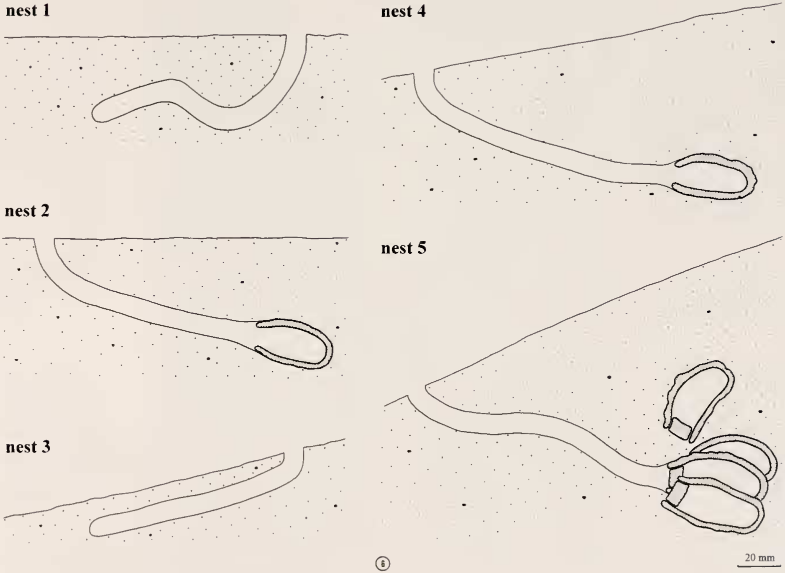

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Fig. 6. Vertical plans of 5 nests of C. *tuberculifer*. For further information see Table 2.

Table 2. Details pertaining to the five nests of *Ceramius tuberculifer* excavated on July 25, 1994 at Peyresq (P) and on July 26, 1994 on the Montagne de Boules (B) respectively. The cell of nest 2 was damaged during excavation. It appeared as if it had not been plugged

Aggregation	Nest No.	Σ females	Σ cells	Condition of the cells	Content of the cells
P	1	1	0	—	—
P	2	1	1	open?	large larva; rests of pollen
B1	3	1	0	—	—
B1	4	1	1	open	rest of a cocoon filled with crumbly earth mixed with cocoon-fragments
B2	5	1	4	sealed with a mud plug	prepupa in a cocoon

left side (Fig. 10). Flight activity of the females started at about 10h00 and on all days was terminated more or less abruptly when the weather became cloudy. Active females were observed until 14h00 at the latest.

The females always entered the nests head first. Wasps that were departing left

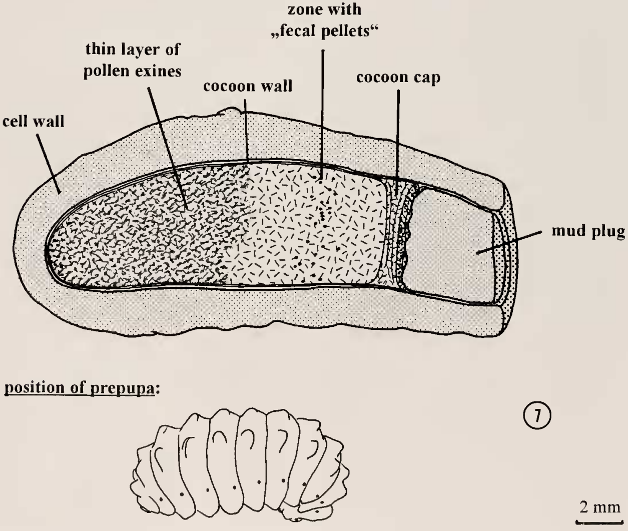
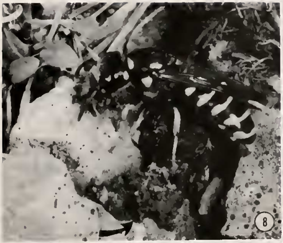
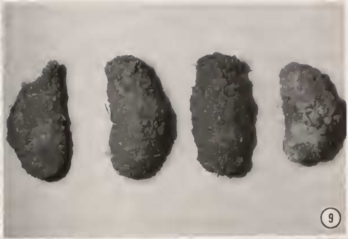
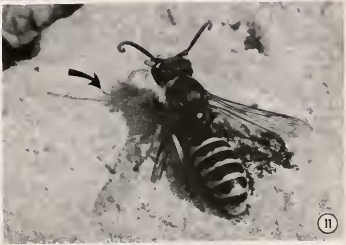
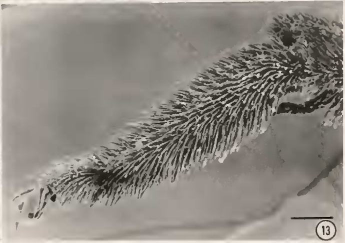


Fig. 7. Schematic representation of a longitudinal section through a mud-cell of *Ceramius tuberculifer* from nest 5. The cocoon contained a prepupa.









Figs. 8–13. Fig. 8. *Ceramius tuberculifer* during nest excavation at Peyresq, 28.7.1994. The female is turning round with a soil-pellet held in her mandibles after she had backed out of the entrance. The pellet-dropping area in the foreground is marked with an arrow. Fig. 9. Constructed mud-cells of *Ceramius tuberculifer* from nest 5 from aggregation B2, 26.7.1994 (length of each side of the squares is 5 mm). Fig. 10. Female of *Ceramius tuberculifer* sheltering under twigs during a period of unfavourable weather at Montagne de Boules, 29.7.1994. Fig. 11. Male of *Ceramius tuberculifer* perching on a sun-exposed stone at Peyresq, 28.7.1994 (arrow pointing at the shadow of the widely opened mandibles). Fig. 12. Female of *Ceramius tuberculifer* visiting a flower of *Teucrium montanum* at Peyresq, 28.7.1994. The anthers touch frons and vertex of the wasp (arrow). Fig. 13. Left foretarsus of a *Ceramius tuberculifer* female from posterior (scale bar = 0.3 mm).

Table 3. Flower visiting records for males and females of *Ceramius tuberculifer* on five days of observation at Peyresq (P) and on the Montagne de Boules (B). (O = >5 observations o = 2–5 observations + = single observation)

Plant taxon	19.7.P		21.7.P		25.7.P		26.7.B		28.7.P		29.7.B	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Lamiaceae LINDL.												
Teucrium montanum L.	O	O	O	O	O	O	O		O	+	O	
Lavandula angustifolia MILLER ssp. *angustifolia*							o		+		O	
Cistaceae JUSS.												
Helianthemum oelandicum (L.) DC. ssp. *alpestre* (JACQU.) BREISTR.					O	O						
Fabaceae LINDL.												
Ononis fructicosa L.							o					

the shaft, likewise, running forward. More than once it was observed that an individual which had vanished into the burrow running forward left the nest head first or was soon afterwards resting in the anterior part of the shaft with its head directed towards the entrance, indicating that they had turned around inside the burrows.

Behaviour of the Males.—Males of *C. tuberculifer* were regularly observed in the area to the northeast of the nesting aggregation P, an area commonly visited by foraging females. Activity of the males started about 10h30. They were moving over the *Teucrium* clumps in a slow, constant flight approximately 0.1 m above the ground. Every few metres (usually 1–3 m, at most 20 m) they interrupted their flight and alighted on sun-exposed stones or dry twigs lying on the ground, where they perched for brief periods (less than a minute). On the perch they maintained a characteristic posture; antennae and wings were raised at about 45° to the median axis of the body and mandibles were opened wide (Fig. 11). Often the males simultaneously rubbed the ventral side of their metasoma with the hind-legs. Sometimes in addition they cleaned the head and the dorsal part of the thorax with the fore-legs. When disturbed, for example by a passing insect, the males resumed their flight. In other cases they started flying anew without an obvious stimulus. After a few metres in flight they alighted on another perch. In this way, they seemed to patrol along more or less constant paths. The same perches were repeatedly visited by males. One particular male covered a complete oval course of approximately 40 m for one and a half times, alternating between flying and perching, before sight of it was lost. Matings were not observed, but frequently the males briefly approached other insects during the patrol flights and from perches. On one occasion a patrolling male flew rapidly towards another flying male, chased it for about 0.5 m before returning to its course. The patrolling behaviour was irregularly interrupted by periods in which the males visited flowers. Around midday males were occasionally observed in the range of the nesting aggregations, where they alighted for a short while on the ground close by the nest entrances. On one morning a male was resting in the shaft of a nest with its head directed towards the nest entrance.

Flower Visiting.—Flower visiting records for imagines of *C. tuberculifer* are presented in Table 3. The most frequently visited plant was *T. montanum* but there was no fidelity to flowers and several times both males and females changed from one

Table 4. Distribution of pollen grains on the exoskeleton of males and females of *Ceramius tuberculifer*. The arithmetic means and the standard errors for the total number of pollen grains per individual and for the percentage of grains found on different parts of the body are given

			Percentage of pollen-grains on		
	n	Σ pollen grains per individual	Vertex and frons	Dorsal part of the mesosoma	Rest of the body
Males	5	368 (±57)	67 (±6) %	12 (±5) %	21 (±4) %
Females	5	132 (±40)	66 (±14) %	10 (±7) %	23 (±8) %

plant species to another during a single foraging trip.

Pollen Gathering.—The crop of three females was distended with pollen, which was suspended in some liquid. Ventriculus and rectum of all dissected individuals contained pollen grains in variable quantities. The pollen-content of ventriculus and rectum of six females consisted of a mixture of pollen from *Teucrium, Helianthemum*, a species of Fabaceae and on a smaller scale also *Lavandula,* species of Liguliflorae and additional unidentified plant taxa. Individual differences existed, however, in regard to the proportion of particular plant taxa. The ventriculus and rectum of four females contained mostly pollen of *Teucrium,* whereas the other samples were dominated either by *Helianthemum* or by an unidentified species of Fabaceae.

When the imagines visited the nototribic flowers of *T. montanum* (i.e. the anthers have a dorsal position in a monosymmetric flower so that regular pollinators are dusted with pollen on their back) their frons and vertex made contact with the anthers (cf. Fig. 12). In consequence the main proportion of pollen on the exoskeleton was located on these parts of the head (Table 4). After having visited several flowers the adults alighted regularly on sun-exposed stones or plants. There they groomed the dorsal and frontal parts of the head with the fore-legs which alternately were moved over it from dorsal/posterior to ventral/anterior. In two cases it was possible to observe that the distal parts of the fore-legs were brought between the mandibles each time after the leg had been wielded over the head and that the mouthparts were moving simultaneously. Fore-tibiae and -tarsi of the females and to a lesser extent of the males form a pollen brush as they are short, thick and densely covered with stiff hairs (Fig. 13).

Parasites.—Imagines of the chrysidid wasp *Chrysis emarginatula* Spinola were common at all nesting aggregations, where they were observed on repeated occasions entering the burrows. The species was not found beyond the close vicinity of the nests. The activity of the adults was influenced to a lesser extent by irradiation and/or temperature than was that of *C. tuberculifer*.

Two female *C. tuberculifer* from Peyresq had the metasoma nearly completely filled with a larva of *Zodion* (Conopidae).The atrial domes of each larva were orientated towards the ventral side of the wasp and had immediate contact with the tracheal sacs of its host. The posterior end of the larva was situated in the first metasomal segment, the anterior end in the sixth. In relation to the median axis of the host the slender fore-end of the larva was orientated to the right. The alimentary tract and the ovaries of the host were compressed on its left ventral side.

A male from Peyresq contained, in the metasoma, a parasitic stage of an unidentified representative of the Mermithidae (Nematoda).

DISCUSSION

The aggregations investigated were smaller than those described by Giraud

(1871) and Ferton (1901), each of which had a few hundred individuals. Other *Ceramius*-species also exhibit a remarkable variation with regard to both nest dispersion and the number of nests in an aggregation (cf. Gess & Gess 1980, 1986, 1988, 1990). Both localities of *C. tuberculifer* were covered with calcareous grassland, which is in accord with the sketchy habitat descriptions of Giraud (1871) and Ferton (1901). At all aggregations investigated the nesting substrate was somewhat friable whereas in the Pyrenees the species was found nesting on solid, clay soil (Ferton 1901).

Afrotropical *Ceramius* use water for softening the soil in nest construction (Gess & Gess 1986, 1988, 1990). The same behaviour was shown by females of *Ceramius* in the Pyrenees (Ferton 1901). In agreement with Giraud (1871) *C. tuberculifer*, nesting in the French Alps, likewise uses a liquid at least for the construction of turret and cells, but this is not necessarily water. Nectar may conceivably be used instead, since none of the dissected females carried water (cf. also Giraud 1863, 1871), but two had their crops completely filled with nectar.

As already indicated by Giraud (1871) and Ferton (1901), *C. tuberculifer* constructs a mud entrance turret. Building a turret probably belongs to the ground pattern (in the sense of Ax 1984: 156) of *Ceramius*, since it has been recorded for members of all species-groups (cf. Gess & Gess 1992) and for all other ground-nesting Masarinae studied to date (cf. Gess & Gess 1980, Houston 1984). Ferton (1901) mentioned that the turrets were always repaired as soon as they had been damaged, whereas reconstruction or repair of a turret was not observed in the Verdon valley, which is in agreement with Giraud (1871).

As described by Giraud (1871) the shafts of the nests in the present study were 50–70 mm long but in contrast to his account they descended obliquely into the ground not vertically. This oblique descent of the shaft is remarkably different from the condition present in the nests of the Afrotropical species of *Ceramius*, the shafts of which are always almost vertical (Gess & Gess 1986, 1988, 1990). In most of the Afrotropical species the shaft has a short bulbous enlargement ("bulb") in the upper part, which allows the imagines to turn round in the burrow (Gess & Gess 1988). Such a bulb is lacking in the nests of *C. tuberculifer*.

The observations regarding the behaviour of the wasps, when excavating their burrows, correspond well with the account by Giraud (1871). Like other *Ceramius* species the females of *C. tuberculifer* back up the shaft with a soil pellet held by their mandibles (cf. Gess & Gess 1980, 1986, 1988, 1990). However, in contrast to the other taxa they do not fly up to discard the pellet but move to the pellet dropping area on foot. The existence of a clearly defined pellet dropping area has only been reported for two members of species group 8 (Gess & Gess 1980, 1988). In other *Ceramius*-species the pellets are spread out over a larger area (Gess & Gess 1980, 1988).

The brood-cells are constructed within a previously excavated cavity, that is they are "mud-cells" in the sense of Gess & Gess (1986). This is in agreement with the descriptions by Giraud (1871) and Ferton (1901). The construction of such mud-cells is probably plesiomorphic within *Ceramius* and occurs in all Afrotropical taxa except for members of species group 8 (cf. Gess & Gess 1992) where it must have been lost secondarily. The variable, more or less asymmetrical shape of the mud-cells of *C. tuberculifer* contrasts with the regular shape recorded for the mud-cells of other *Ceramius* species (cf. Gess & Gess 1980, 1986, 1988, 1990). As reported by Giraud (1871), the first cell terminates the main shaft of the burrow, a character shared with most of the other *Ceramius* species with the exception of *C. lichtensteinii* (cf. Gess & Gess 1988). Perennial nests have been recorded for most species which construct mud-cells (Gess & Gess 1988). Two findings suggest that this is also the case in *C. tuberculifer*: Firstly, two cells had fragments of cocoon-material embedded in their walls and mud-plugs, which indicates that they were constructed after imagines had already emerged from this nest. Secondly, one nest contained a female along with an old cell, from which an imago had already emerged.

Ferton (1901) reported that the provisioned cells were sealed with a mud-plug. In contrast, Giraud (1871) found all cells to be open, irrespective of their pollen content and the development of the larvae. Furthermore, the cell of nest 2 was probably not sealed, although it contained a large larva. Open cells with larvae occur occasionally also in *C. lichtensteinii* (Gess & Gess 1980). This may be due to unfavourable foraging conditions which bring about delayed provisioning after deposition of the egg. The effect of this delay would be that the larva hatches and starts feeding before provisioning and sealing of the cell is completed (Gess & Gess 1980).

Brood-cells of *Ceramius* containing prepupae have been described only in *C. lichtensteinii* (Gess & Gess 1980) and *C. rex* Saussure (Gess & Gess 1988). With 4–8 mm and 3 mm respectively the space between the mud-plug and the cocoon cap is much longer in both species than in *C. tuberculifer*. The thin brittle yellowish layer of pollen-exines on the inner wall in most of the lower half of the cocoon of *C. tuberculifer* is probably the meconium. A similar thin faecal layer is deposited over the distal three-fifths of the cocoon of *Paragia tricolor* Smith (Masarinae), though there are often also thick scales deposited at its distal end (Houston 1984). A comparably thin meconium occurs in *Euparagia scutellaris* Cresson (Euparagiinae) (cf. Torchio 1970). In contrast the meconium of *Pseudomasaris* is restricted to the posterior end of the cocoon, where the excrements form a compressed cake, about half as deep as wide, with a flat surface, which is perpendicular to the walls of the cocoon (Torchio 1970, cf. Hicks 1927).

Although pairing was not observed, it can be assumed that the males were seeking mates in the foraging area of the females. Likewise males of the Afrotropical *Ceramius* search for potential mates at resources that are regularly visited by females, for example water (cf. Gess & Gess 1980, 1988) and forage plants (cf. Gess & Gess 1990). Males of *C. tuberculifer* interrupt their patrol flights regularly in order to perch for brief periods. The characteristic behaviour of *C. tuberculifer* males on the perch, especially the opened mandibles, and the rubbing of the ventral surface of the gaster with the hind-legs, may conceivably indicate the release of a pheromone. Comparable behaviours are shown by males of some species of *Polistes* (Vespidae) while chemically marking their territorial perches (cf. e.g. Beani & Calloni 1991, Wenzel 1987). The use of pheromones in courtship behaviour has not been reported for any representative of the Masarinae (cf. e.g. Alcock et al. 1978, Alcock 1985, Gess & Gess 1988, 1990, Hicks 1929, Houston 1984, Longair 1987). Males of *Pseudomasaris maculifrons* (Fox) (Alcock 1985: Fig. 2) and *P. vespoides* (Cress.) (Hicks 1929), however, also perch and whilst so doing slightly spread their wings. At least in this respect their behaviour is similar to that of *C. tuberculifer*.

The Afrotropical taxa of *Ceramius* are oligolectic to a high degree. They obtain pollen from either Mesembryanthemaceae, Asteraceae or Fabaceae (Gess & Gess 1989, 1990). Members of the same species group exhibit a marked fidelity to flowers of a single plant family (Gess & Gess 1989). This does not seem to be the case in species group 7, with *Ceramius tuberculifer* being obviously polylectic. In addition other members of the species group have been recorded visiting flowers of Lamiaceae, Fabaceae and Apiaceae (Richards 1963). These records can be misleading, however, since they do not verify that the visited plants are utilized as a pollen source (Gess & Gess 1988).

The occurrence of *Teucrium montanum* seems to be of particular importance for *Ceramius tuberculifer*. At both nesting sites the plant was strikingly more abundant than in the surrounding areas, its flowers were visited most frequently and it was most common in the majority of the pollen samples from the alimentary tract. During the visits to the nototribic *Teucrium* flowers the anthers come into close contact with the vertex and frons of the imagines, so that most of the pollen is deposited on these parts of the body. Afterwards it is drawn towards the mouth by grooming movements of the brush-like forelegs and is finally ingested. This behaviour differs remarkably from the pollen gathering methods employed by other *Ceramius* species and most of the other Masarinae, which either use their forelegs to agitate the anthers and draw the pollen towards their mouth or ingest pollen directly from the anthers (Gess & Gess 1989, 1990b, cf. Neff & Simpson 1985, cf. Torchio 1970). *Celonites abbreviatus* Villers is an exception for the imagines gather pollen from nototribic flowers of different Lamiaceae in a manner which is quite similar to the behaviour of *C. tuberculifer* (cf. Schremmer 1959, cf. Müller in press). The similarities are probably due to convergent behavioural adaptations to a nototribic pollen presentation (cf. Müller in press). Comparable pollen-harvesting methods have also been independently developed several times in some taxa of Apiformes, which likewise collect pollen at nototribic flowers (Müller in press). In contrast to these taxa, imagines of *C. tuberculifer* neither show specialized behaviours to improve the release of pollen from the anthers nor do they have particular morphological devices (cf. Schremmer 1959, cf. Müller in press). (The brush-like forelegs of *C. tuberculifer* cannot be interpreted as a morphological adaptation to pollen gathering from nototribic flowers, since they occur in all Masarini (Richards 1962: 35) and therefore probably represent a plesiomorphic character.)

Chrysis emarginatula has already been reported as a parasitoid of *C. tuberculifer* by Ferton (1901). In addition Linsenmaier (1968) found this chrysidid associated with an undeterminated *Ceramius* species in Spain. Likewise the second member of the *C. emarginatula* group, *C. tingitana* Bischoff, has exclusively been established together with *Ceramius* (Linsenmaier 1968). Larvae of *Zodion* (Conopidae) have not been recorded as endoparasites of any representative of the Masarinae before (cf. Smith 1966). Previously, the taxon has mainly been associated with various species of Apiformes and only rarely with *Podalonia* ("Sphecidae") and *Odynerus* (Eumeninae) (Smith in litt. 1994).

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